

Bergmann's Rule and the Thrifty Genotype

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KEY WORDS diabetes; thrifty genotype; body weight; Polynesians

ABSTRACT One of Roberts' key contributions was his work demonstrating the applicability of several ecological rules to human populations (Roberts [1953] *Am. J. Phys. Anthropol.* 11:533-558; [1978] *Climate and Human Variability*, 2nd ed., Menlo Park, CA: Cummings). His finding that average body weight systematically covaries with mean annual temperature was widely taken as confirmation of Bergmann's rule for humans. More recently his findings on weight and temperature have been extended and confirmed (Ruff [1994] *Yrbk. Phys. Anthropol.* 37:65-407; Katzmarzyk and Leonard [1995] *Hum Biol Council Program Abstracts* 132) although the strength of the association may be decreasing when considering more recent surveys (Katzmarzyk and Leonard [1995]). Roberts noted in 1953 that Oceanic populations may be somewhat of an exception to Bergmann's rule, and we propose that Neel's ([1962] *Am. J. Hum. Genet.* 14:353-362) thrifty genotype model may account for some of the deviation from predicted weights among these populations.

We provide an updated version of the thrifty genotype model, suggesting that selection for energetic efficiency may have occurred for some Oceanic populations during the voyaging to and settlement of their island homes. Under conditions of modernization the thrifty genotype may be manifesting as high rates of obesity and NIDDM among Polynesians and Micronesians. First, using measurements of adult male weight from 19 Oceanic populations, we demonstrate the extreme nature of their deviation from predicted weight based on Roberts' regression of weight on mean annual temperature. Next, we regress the deviations from predicted weight on NIDDM prevalence for these 19 populations, producing a highly significant regression ($R^2 = 0.46$; $P < 0.001$), consistent with expectations if the thrifty genotype is responsible for the high weights. *Am J Phys Anthropol* 104:201-210, 1997. © 1997 Wiley-Liss, Inc.

Roberts is best known in anthropology for his important work advancing knowledge about human genetics (e.g., Roberts, 1986; Janicijevic et al., 1994). However, for some biological anthropologists his analyses of the relationship of morphology to climate were also a significant contribution to the study of human adaptation. More clearly than most other workers, Roberts demonstrated the applicability of certain ecological rules to human populations. Most notably, his analyses of measurements from a large

number of geographically diverse populations demonstrated that weight and other measurements are systematically correlated with climate (Roberts, 1953, 1978). Many of the populations included in Roberts' analyses have been affected by socioeconomic modernization since the measure-

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Received 22 February 1996; accepted 5 November 1996.

ments were taken, some of the surveys dating from the first decades of this century. Body weights in particular have been strongly affected by the changes associated with modernization (Baker, 1986; Bindon, 1995; Bindon and Baker, 1985). In this paper we explore the extent to which the thrifty genotype hypothesis applied in the context of modernizing Pacific populations may account for some of the more extreme deviations from the relationship between body weight and environmental temperature calculated by Roberts.

BERGMANN'S RULE

One of the primary ecological principles Roberts was testing in the early 1950s was Bergmann's rule (Roberts, 1952, 1953), paraphrased by Roberts as "within a polytypic warm-blooded species, the body size of a subspecies usually increases with decreasing mean temperature of its habitat" (1953:551). Different measurements of body size were used to assess Bergmann's rule by various contemporaries (e.g., Newman, 1953; Schreider, 1950), but Roberts focused on weight as the critical measurement of body size. As Roberts notes, a very small percentage of published studies provide information about average weight (e.g., just over 3% of the studies on African populations available in the early 1950s). He restricted the series he considered to those having more than 20 individuals of the same sex. Under these constraints, and adding in some unpublished data, Roberts was able to assemble comparable measurements for males from 116 populations and females from 33 populations. He grouped the populations into major geographic units, to which he referred, in the tradition of the time, as "continental groups" or "subspecies." The studies on which Roberts based his sample were conducted during the first half of the 20th century, with none of them occurring more than a few years after World War II, and most occurring before the war. Thus, the vast majority of the populations had yet to experience any substantial effects of socioeconomic modernization.

Roberts noted that when considering weight as the general measure of human body size, Bergmann's rule is applicable

both between and within "subspecies," and for the species as a whole. This latter point is illustrated in his regression of weight on mean annual temperature for his total sample of adult males from 116 populations. He calculated a linear regression for the men which is given by:

$$\text{Weight (in kilograms)} = 75.6 - 0.305$$

$$\times \text{Mean Annual Temperature (in } ^\circ\text{F)}.$$

This regression is highly significant at $P < 0.001$, and $R^2 = 0.36$. Of interest to our current effort, in his Figure 7, Roberts plotted average adult male weight against mean annual temperature for all 116 populations (1953:543). In this figure, the two points lying farthest above the line are the two Polynesian populations included in the sample: New Zealand Maoris and Native Hawaiians. All four of his Melanesian groups also lie above the line. In examining differences among "continental groups," Roberts notes that "in Oceania, Polynesians seem to be characterized by higher weights than Melanesians" (1953:537). In another analysis (his Table 4), Roberts notes that the Polynesians have the highest average weight after adjusting for temperature and stature. It should be noted that he advocates extreme caution in trying to interpret results based on two Polynesian and four Melanesian groups.

More recently Roberts' overall findings have been confirmed by Ruff (1994) and Katzmarzyk and Leonard (1995). Ruff presents associations between body measurements, including weight, and absolute degrees of latitude as a proxy for temperature. He finds a strong association ($r = 0.607$, $P < 0.001$) when analyzing weight and absolute value of latitude associations for the 56 series (31 male, 25 female) of measurements he assembled (Ruff, 1994). The magnitude of this result is very similar to that found by Roberts (1953) for males ($r = -0.600$, $P < 0.001$), and somewhat less than for females ($r = -0.807$, $P < 0.001$). The direction of the association is of course reversed since the association between temperature and latitude is inverse. Ruff's series include some samples measured in the 1960s and 1970s that were not available to Roberts.

Katzmarzyk and Leonard (1995) updated Roberts' work by compiling a series of 206 male and 172 female samples from around the world and calculating correlations between mean annual temperature and several body measurements. Many of the sources for their series are based on surveys conducted in the 1970s and 1980s, making this a more current analysis than that of either Roberts or Ruff. They found that the correlation between weight and temperature for males is of lower magnitude than that calculated by Roberts ($r = -0.255$, $P < 0.001$ vs. $r = -0.600$), and they note that their linear regression of weight on temperature has a smaller (i.e., flatter) slope than the regression calculated by Roberts. They suggest that this difference is due to increasing weights over the last several decades, especially among tropical, hot weather populations. While this may be a general trend across tropical populations, it is undoubtedly not universal, and among those populations showing weight increases, it is certainly more pronounced in some populations than others. It is this phenomenon, the flattening of the regression slope caused by extreme weight increases in some hot weather populations influenced by modernization, that we wish to address.

THE "THRIFTY" GENOTYPE

Neel (1962) proposed the "thrifty" genotype model to explain why non-insulin dependent diabetes mellitus (NIDDM) occurs at such high frequencies in some populations. Both Neel and others have updated this model in the face of increasing information about the metabolism of NIDDM (Cahill, 1979; Neel, 1982; Bindon, 1983; Baker, 1984; Zimmet, 1989). It should be stressed that NIDDM is a condition with extremely complex etiology. The thrifty genotype model is not meant to account for NIDDM in all populations, but rather, the evolutionary history of certain populations such as Polynesians and Amerindians may incorporate situations creating a strong selective advantage for individuals with the thrifty genotype. Other populations such as Asian-Indians and European-Americans who also manifest substantial rates of NIDDM may be express-

ing the results of very different genotype-environment interactions.

Figure 1 presents our modification of the thrifty genotype model used by Zimmet et al. (1990) to account for high frequencies of obesity and NIDDM among modernizing Oceanic populations. This model remains highly speculative, although there are biochemical and clinical studies supporting each of the elements we propose. The thrifty genotype model suggests that NIDDM results from a genetic predisposition for the efficient utilization of dietary energy, effected by an exaggerated secretion of insulin by the beta cells of the pancreas in response to carbohydrate intake, a response known as hyperinsulinemia (Zimmet, 1989).

The transport of glucose into cells is facilitated by insulin bound to specific insulin receptor sites on cell walls. Maximum glucose uptake occurs when 10–20% of the receptors are bound with insulin, which is easily achieved with normal insulin secretion. Increased metabolic efficiency for thrifty genotype individuals may result from an extended period of high circulating insulin levels resulting in enhanced glycogen formation, particularly in the peripheral muscle cells that account for about 85% of glucose clearance (Olefsky et al., 1982; DeFronzo and Ferranini, 1982; Bjorntorp et al., 1971).

A potentially more significant effect of hyperinsulinemia results from the lipogenic effect of insulin. Circulating insulin activates lipoprotein lipase on the capillary surfaces which hydrolyzes triglycerides in the plasma to facilitate transfer into adipose cells (McGarry, 1992). Insulin also inhibits hormone sensitive lipase which is instrumental in hydrolyzing triglycerides stored in adipose tissue and releasing fatty acids into plasma (McGarry, 1992). The net result of this process is to increase the storage of energy in adipose tissue. Both the magnitude and duration of this effect are likely to be increased in hyperinsulinemic individuals.

As originally conceptualized by Neel, populations cycling through periods of feast, famine, and energy balance would be subjected to selection favoring the survival and reproduction of individuals with the thrifty genotype. The negative consequences of the

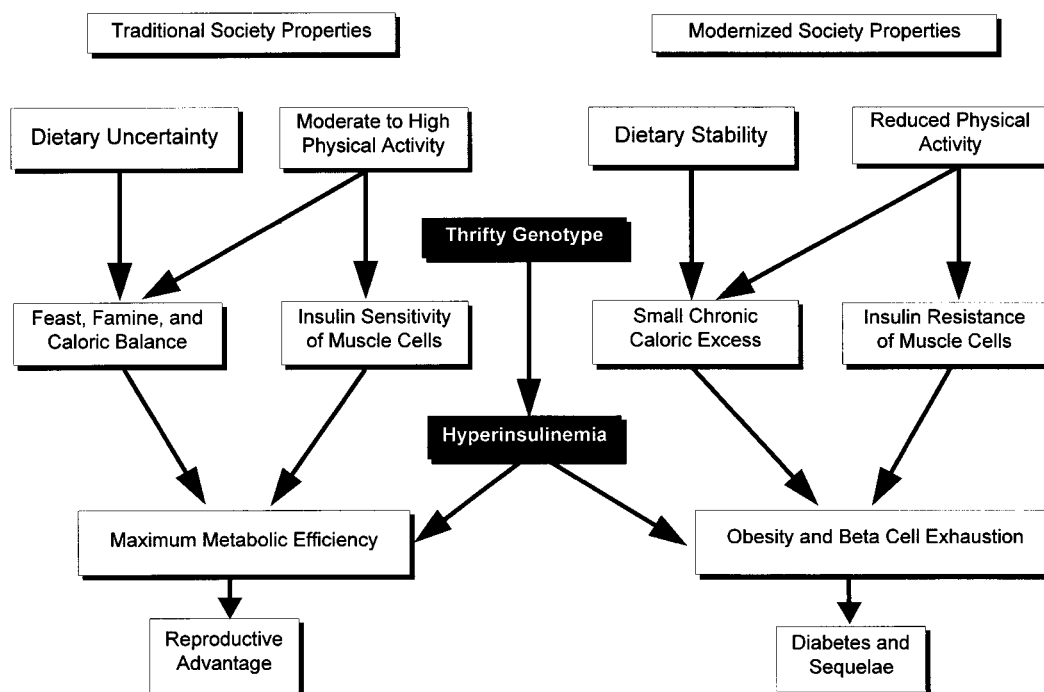


Fig. 1. A speculative model of modernization and the "thrifty" genotype.

thrifty genotype, including NIDDM, would be restrained by energetic balance and periodic famine. In our update, we speculate that NIDDM could be kept in check in traditional populations by physical activity. Several studies have shown improved insulin effectiveness and glucose tolerance in response to physical training and exercise (Krotkiewski et al., 1985; Minuk et al., 1981). Insulin receptors on the peripheral muscle cells of NIDDM patients become more sensitive to binding with circulating insulin with increasing physical activity (DeFronzo and Ferrannini, 1982). Increases in activity also tend to decrease the amount of insulin released by the pancreas in response to a glucose load, reducing hyperinsulinemia and its physiological effects (DeFronzo, 1982). Both prospective (Helmrich et al., 1991) and retrospective (Frisch et al., 1986) longitudinal studies have indicated that increasing physical activity is associated with reduced incidence and prevalence of NIDDM, especially in individuals at high risk for developing the disease (Helmrich et al., 1991). Thus,

decreases in physical activity associated with modernization may play a key role in the development of NIDDM among individuals with the thrifty genotype.

Obesity frequently occurs in conjunction with NIDDM. However, several studies have illustrated that obesity is neither a necessary nor sufficient condition to produce NIDDM. Asian Indians in Fiji have very high rates of NIDDM but very low rates of obesity (Zimmet et al., 1990). In Pacific populations with substantial obesity rates, Zimmet and colleagues have demonstrated that there is more NIDDM than could be accounted for by the obesity (Zimmet et al., 1977a, 1981), leading them to suggest a key role for activity in NIDDM etiology. Our model speculates that in those populations that have undergone selection for the thrifty genotype, obesity and NIDDM co-occur because of the underlying metabolic peculiarities (energetic efficiency and hyperinsulinemia predisposing to lipogenesis), *not* because one causes the other.

In the case of some Oceanic populations, the cycling of feast, famine, and energy balance would have begun with their voyages of settlement across the Pacific Ocean, and would have been maintained over the ensuing millennia through continued voyaging to maintain trade relationships and by periodic crop-destroying tropical storms. Speculation about the details of these processes for Polynesian populations is available elsewhere (Prior, 1977; Bindon, 1983, 1988, 1995; Bindon et al., 1991; Baker, 1984; Zimmet et al., 1990; McGarvey, 1994). In some of these populations, the process of modernization has reduced the likelihood of famine and reduced the level of physical activity required for subsistence. As an example of the former, within the last 5 years major storms have produced substantial subsistence disruptions for villages in Western and American Samoa. Prehistorically, such episodes could have served as reinforcement for selection for the thrifty genotype. However, in both recent cases, the severity of these disruptions was tempered by assistance from the international aid community and increased cash and food remittances from relatives who have migrated from Samoa. Additionally, cross-sectional studies suggest that for many if not most individuals in Oceanic populations, physical activity diminishes with socioeconomic modernization (Pelletier, 1984; Schendel, 1989; Zimmet et al., 1977a, 1981; Bindon, 1995). As a result of these changes associated with modernization, some Pacific populations previously selected for the thrifty genotype may experience high rates of obesity, NIDDM, and its sequelae.

METHODS AND TECHNIQUES

In order to investigate the deviations from Bergmann's rule that may be associated with the thrifty genotype, we have assembled measurements on males from a small series of Oceanic populations. If the thrifty genotype is underlying the more extreme deviations from Roberts' regression of weight on temperature, there should be a strong association between the prevalence of NIDDM in a population and the magnitude of deviation from weight predicted by temperature.

Table 1 presents average values of weight, NIDDM prevalence, and mean annual temperature from literature sources and a 1992 survey in American Samoa for males from 19 Oceanic groups [11 Polynesian, four Micronesian, two Austronesian (AN) Melanesian, and two Non-Austronesian (NAN) Melanesian]. The limited nature of this sample recalls Roberts' problems with assembling an adequate series with weight measurements. While averages of weight or NIDDM prevalence are available for many more Oceanic groups than presented here, it is rare to find both data points published for a population. Studies that present average weights rarely have accompanying information about NIDDM, and virtually all of the NIDDM prevalence studies for the past 15 years present body mass index ($BMI = \text{weight in kg}/[\text{height in meters}]^2$), but not weight—although it must be measured to calculate BMI. For the purposes of this analysis, only these 19 groups could be characterized for both variables, and weight for several of these groups has had to be calculated from BMI using stature measurements done on the same populations by workers other than those who surveyed for NIDDM (Fijians, Solomon Islanders, and Kiribati). All of the measurements were made on individuals over 18 years of age, although 20 was the lower limit for some of the studies. Females have been excluded because Roberts did not calculate a weight and temperature regression for the limited series of females he assembled.

The populations have been categorized into more traditional or more modernized groups on the basis of how traditional their lifestyle was at the time the survey was taken. These assessments of traditional vs. modernized have been made by the original authors, using a variety of techniques usually not discussed in the articles. Most of the authors are using the same technique used in the early days of the Samoan Studies Project, categorizing lifestyle on the basis of area of residence. The modernizing and urban populations generally have higher weights and rates of NIDDM than the more traditional groups. Among Polynesians the Puka Pukans stand out as being exceptionally light with low rates of NIDDM, perhaps

TABLE 1. Ethnicity, average weight, diabetes prevalence, and mean annual temperature for adult males (≥ 18 years of age) from 19 Oceanic populations

Population	Ethnicity	N	Average weight (kg)	NIDDM (%)	Mean annual temp. (°F)	Source
Relatively rural or traditional groups						
Fiji Melanesians	Melanesian, AN	239	74.0	1.7	77.2	Clegg, 1989; King et al., 1984
Solomon Islands	Melanesian, NAN	173	60.7	0.0	81.5	Friedlaender, 1987; Eason et al., 1987
Kiribati	Micronesian	469	70.6	3.6	82.9	King et al., 1984; Lewis, 1981
Solomon Islands	Micronesian	140	72.6	4.3	81.5	Eason et al., 1987; Lewis, 1981
Puka Puka	Polynesian	188	67.9	0.5	82.2	Prior et al., 1966
Tokelau	Polynesian	252	74.8	3.9	82.2	Prior and Stanhope, 1980; Stanhope and Prior, 1980
Tonga, Foa	Polynesian	196	75.3	4.6	74.2	Prior, 1977
Tuvalu, Funafuti	Polynesian	226	74.4	1.3	82.9	Zimmet et al., 1977a
Western Samoa	Polynesian	358	76.7	2.8	79.1	Zimmet et al., 1981; Pelletier, 1984
Modernizing, migrant, or urban groups						
Fiji Melanesians	Melanesian, AN	401	75.4	4.8	77.2	Clegg, 1989; King et al., 1984
Solomon Islands	Melanesian, NAN	433	60.7	0.0	81.5	Friedlaender, 1987; Eason et al., 1987
Kiribati	Micronesian	906	77.9	8.1	82.9	King et al., 1984; Lewis, 1981
Nauru	Micronesian	107	85.0	31.8	81.9	Zimmet et al., 1977b
American Samoa	Polynesian	135	84.8	27.2	80.0	Unpublished Data, 1992
New Zealand Maoris	Polynesian	92	81.0	11.9	59.0	Prior et al., 1964
Rarotonga	Polynesian	243	75.2	4.5	74.7	Prior et al., 1966
Tokelau in NZ	Polynesian	493	80.0	3.7	82.2	Prior et al., 1974; Stanhope and Prior, 1980
Tonga, Nuku'alofa	Polynesian	176	83.5	5.7	76.1	Prior, 1977
Western Samoa	Polynesian	325	80.1	12.6	79.1	Zimmet et al., 1981; Pelletier, 1984

because the 1964 survey caught them at a time when they had very limited contact with the outside world (Prior et al., 1966). The only groups with no cases of adult male NIDDM are the rural and urban Solomon Island NAN Melanesians. On the other end of the scale, the Nauruans and American Samoans have extremely high average weights and NIDDM prevalences. In Nauru, the exceptional wealth (\$30,000 per capita in 1977) created by nationalizing the phosphate industry in the 1960s quickly altered lifestyle, resulting in high rates of obesity and NIDDM (Zimmet et al., 1977b). In American Samoa, a combination of U.S. governmental involvement in economic development since the mid 1960s and remittances from kin living in Hawaii and mainland U.S. have resulted in one of the more affluent Oceanic populations after Nauru.

RESULTS

The temperature values in the table have been used to calculate predicted weights from Roberts' summary regression line [weight = $75.6 - (0.305 \times \text{temperature})$].

Even the relatively traditional populations have weights that are substantially above the values predicted by Roberts. Figure 2 provides a scatter plot of average adult male weight against temperature for the 15 Oceanic groups with Roberts' regression line drawn in for reference. All of the points fall substantially above the regression line, confirming Roberts' earlier observation about the deviation of Oceanic populations based on his sample of six surveys. The closest points to the line are the two NAN Melanesian groups, followed by the other eight rural or more traditional groups plus the Rarotongans and the urban Fiji Melanesians. The Rarotongans were measured in 1964, early in their exposure to modernization, and the AN Melanesians in Fiji appear to exhibit a different pattern of weight gain from the Polynesians and Micronesians, as remarked by Roberts in 1953.

Figure 3 presents a plot of the deviations from weight predicted by Roberts' regression against NIDDM prevalence for the 19 groups. As the scatter shows, there is a strong tendency for increasing deviation in weight

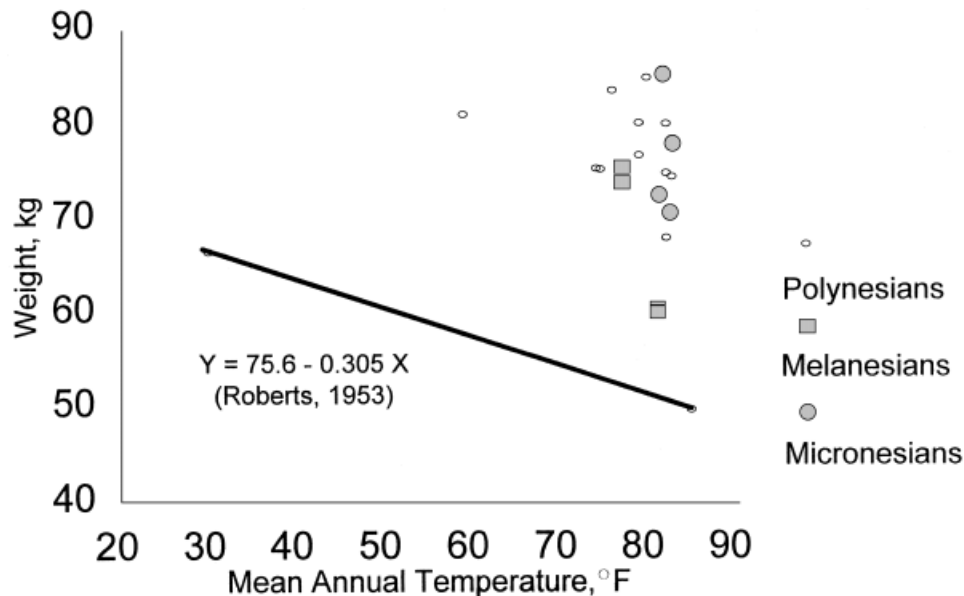


Fig. 2. Average weights of adult males from 19 Oceanic populations plotted against mean annual temperature.

to be associated with increasing NIDDM prevalence. A simple linear regression of the weight deviation on NIDDM prevalence produced a highly significant regression with an adjusted R^2 of 0.46 ($P = 0.0008$). The strength of this association is influenced by the two clusters of points at the low and high end of both distributions. However, the nature of the association appears well demonstrated by the plot of points. The regression line is plotted on the figure for reference. The extreme outliers on the low side from this regression are the NAN Melanesians, who had no NIDDM and very low weights. Above the regression line, the urban Tonga sample from Nuku'alofa, the Tokelau migrants to New Zealand, and an urban group in Kiribati stand out. In the natural history of NIDDM within a population, increases in obesity prevalence usually precede increases in NIDDM by a decade or more, and the deviations of these three groups may be due to their being measured relatively early in their exposure to a modern, relatively sedentary lifestyle. Overall, Figure 3 documents a very strong association between NIDDM and deviation from predicted weights for the 19 populations.

DISCUSSION

Before considering the implications of our findings, we must discuss some limitations. The sampling technique used to assemble our series of populations is the same as that used in virtually all of the surveys cited: opportunistic sampling. There is little assurance that the populations we have chosen are representative of relatively traditional and modern segments of Polynesia, Micronesia, and Melanesia. There is also little assurance that the individuals within each study are representative of the population from which they were drawn. There is too little information given in the publications to estimate direction or magnitude of any sampling bias that might exist. For this reason, the various surveys have been taken at face value, without an attempt to establish representativeness. This acceptance of sampling is exactly what has been done in all the other such works (Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1995). Perhaps more critical to our hypothesis is the absence of age-specific data for weight and NIDDM prevalence across the populations, preventing us from presenting age-adjusted

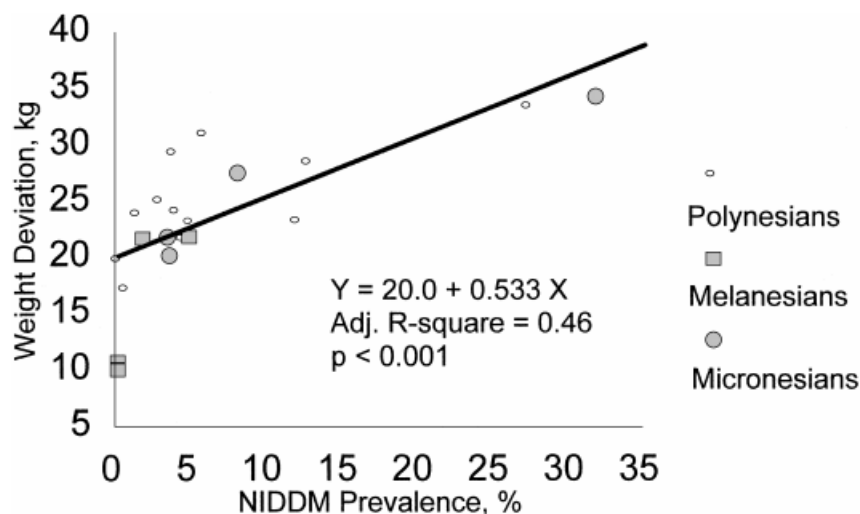


Fig. 3. Deviation in weight from Roberts' (1953) prediction of weight based on mean annual temperature for adult males from 19 Oceanic populations plotted against prevalence of NIDDM.

averages. Both of our outcome measures have distinct age-related patterns, and our presentation would certainly have greater validity if we could use age-adjusted values.

These limitations notwithstanding, there are several points to be made. The weight data on Pacific populations consistently show that most Polynesian and Micronesian populations develop very high body weights when they engage in modern, sedentary lifestyles. These average body weights tend to exceed those found in any other population, irrespective of climate. Some studies suggest that AN Melanesians, those who show a higher degree of relatedness to Polynesian and Micronesian populations, also have a tendency to gain weight in modernizing settings but not to the same extent found in Polynesian and Micronesian groups (Zimmet et al., 1990). By contrast, NAN Melanesians remain relatively lightweight and almost free of diabetes in both rural and urban settings.

While there is a tendency for weight gains in all of these groups to be associated with higher NIDDM prevalence, there is not a one-to-one correlation. If obesity were a necessary precursor condition or a cause of NIDDM, it could be argued that the association demonstrated in our Figure 3 was the result of reversing dependent and indepen-

dent variables. However, as noted above, several workers have demonstrated that obesity is not sufficient to account for the high rates of NIDDM found among Polynesians. In Figure 3, demonstrating the association between NIDDM prevalence and deviation from Roberts' predicted weight, we are not attributing causality to NIDDM. Rather, as noted in the discussion of our model of the thrifty genotype, we suggest that the underlying metabolic shift causes both obesity and NIDDM under modernizing conditions. A key factor in the development of *both* obesity and NIDDM may be a reduction in activity levels. In examining NIDDM among Melanesians and Indians in Fiji, Taylor et al. (1984) demonstrated a significant independent effect of activity on NIDDM *after adjusting for age, obesity, and rural vs. urban status*. These data further support the role of decreasing activity in the expression of NIDDM by individuals with the thrifty genotype, as depicted in our model in Figure 1.

Both obesity and NIDDM tend to be more common among modernizing Polynesians and Micronesians than Melanesians. This is consistent with a model of the settlement of Oceania that posits a major barrier between the early Melanesian homeland and the early Polynesian and Micronesian colonies.

This barrier could have consisted of long, open ocean stretches against prevailing winds and currents which buffer both Polynesia and Micronesia from Melanesia. The proto-Polynesian and proto-Micronesian sailors who conquered this barrier may have sailed through a genetic bottleneck strongly selecting for survival in the face of cold stress and starvation (see Baker, 1984; Houghton, 1990). The genetic remnants of this bottleneck episode may be what accounts for the extreme response to modernization seen in Polynesian and Micronesian populations on the one hand and less extreme response among Melanesians (and especially those Melanesians with little or no Polynesian or Micronesian admixture, the NAN Melanesians) on the other.

Thus it may be that the relationship of body weight to temperature which Roberts found would closely resemble that found in our more recent results provided corrections were made for the thrifty genotype in some groups which exhibit the unusual ability to gain weight very rapidly in a modernizing context. Such a correction is made, in effect, by our highly significant regression in Figure 3, where the NIDDM prevalence serves as proxy for the modernization by thrifty genotype interaction. However, it is likely that the Oceanic groups would still plot substantially above the regression line for all of Roberts' populations as indicated by the intercept in our regression, almost 20 kg above the Roberts' line at 0% NIDDM. Some of this deviation may be accounted for by factors associated with the physiology of cold stress, as suggested by Houghton (1990), which we plan to explore in the near future.

ACKNOWLEDGMENT

Some of the ideas presented in this paper were stimulated by PTB's participation in The Thrifty Genotype Hypothesis: Concepts and Evidence After 30 Years, a symposium sponsored by the Australasian Clinical Nutrition Society (NZ), December 8–9, 1994, University of Auckland, New Zealand.

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